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Klebsiella pneumoniae Produces No Histamine: *Raoultella planticola* and *Raoultella ornithinolytica* Strains Are Histamine Producers

Masashi Kanki,* Tomoko Yoda, Teizo Tsukamoto, and Tadayoshi Shibata

Osaka Prefectural Institute of Public Health, Higashinari-ku, Osaka 537-0025, Japan

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Histamine fish poisoning is caused by histamine-producing bacteria (HPB). *Klebsiella pneumoniae* and *Klebsiella oxytoca* are the best-known HPB in fish. However, 22 strains of HPB from fish first identified as *K. pneumoniae* or *K. oxytoca* by commercialized systems were later correctly identified as *Raoultella planticola* (formerly *Klebsiella planticola*) by additional tests. Similarly, five strains of *Raoultella ornithinolytica* (formerly *Klebsiella ornithinolytica*) were isolated from fish as new HPB. *R. planticola* and *R. ornithinolytica* strains were equal in their histamine-producing capabilities and were determined to possess the *hdc* genes, encoding histidine decarboxylase. On the other hand, a collection of 61 strains of *K. pneumoniae* and 18 strains of *K. oxytoca* produced no histamine.

Histamine fish poisoning (HFP) caused by eating spoiled fish happens throughout the world (2, 3). HFP is usually a rather mild illness; however, serious complications, such as cardiac and respiratory manifestations, occur rarely in individuals with preexisting conditions (12). The implicated fish are mainly of the families *Scomberesocidae* and *Scombridae* (the so-called scombroid fish) and contain large amounts of histamine (21). A hazardous level of histamine is produced by the microbial decarboxylation of the free histidine in the muscular tissue of fish. Enteric bacteria have been reported to be the dominant histamine-producing bacteria (HPB) in fish (19). In 1979, Taylor et al. reported that histamine-producing *Klebsiella pneumoniae* strain T2 was isolated from spoiled tuna sashimi (20). *K. pneumoniae* has been the best-known HPB ever since that report, and *Klebsiella oxytoca* is also known as an HPB from fish (13). However, *K. pneumoniae* strain T2 was later sent to the American Type Culture Collection (now in Manassas, Va.) and identified as *Klebsiella planticola* (ATCC 43176) in 1987. This strain has been reported to possess the *hdc* genes, encoding pyridoxal phosphate-dependent histidine decarboxylase (8).

In 1981, Bagley et al. proposed the name *Klebsiella planticola* for "*Klebsiella* species 2" to distinguish it from both *K. pneumoniae* and *K. oxytoca* (1). Moreover, *K. planticola*, together with *Klebsiella ornithinolytica* and *Klebsiella terrigena*, was classified in the new genus *Raoultella* in 2001 (5). Nevertheless, *Raoultella planticola* cannot be distinguished from *K. pneumoniae* or *K. oxytoca* by using commercialized systems, such as API 20E (Biomérieux, Marcy l'Etoile, France). Additional tests are necessary to differentiate *R. planticola* from *Klebsiella* species (14, 15). Similarly, in 1989 the name *Klebsiella ornithinolytica* was proposed for "NIH group 12" at the National Institute of Health, Tokyo, Japan, and "*Klebsiella* group 47" at the Centers for Disease Control, Atlanta, Ga., which showed positive reactions in indole production and ornithine decarboxylase tests (6, 18). *K. ornithinolytica* was also classified in the genus *Raoultella*.

K. pneumoniae and *K. oxytoca* had been shown to be HPB in several reports, whereas *R. planticola* had not been reported as an HPB except in the case of strain ATCC 43176 (4, 10, 11). It is assumed that *R. planticola* had been misidentified as either *K. pneumoniae* or *K. oxytoca* due to a lack of *R. planticola* in the databases of commercialized systems. So we isolated nonmotile strains of HPB from fish with the agar used by Niven et al. (17) and identified them as either *R. planticola* or *R. ornithinolytica* by use of the identification system of Monnet and Freney (14). Moreover, we investigated nonmotile strains from stool specimens, provided strains, and reference strains for their histamine-producing ability. The purpose of our study was to clarify the identification of histamine-producing *Raoultella* strains and investigate the histamine-producing capability of *Raoultella* strains.

MATERIALS AND METHODS

Bacterial strains and identification system. A total of 145 strains were examined. Twenty-seven nonmotile strains were isolated from fish, such as tuna, bonito, and sardines, with the agar used by Niven et al., which contains histidine and detects HPB (17). These strains showed the purple halo characteristic of a histamine-positive reaction on agar plates. Eighty-eight nonmotile strains were isolated from stool specimens with salmonella-shigella agar. The above-mentioned strains from fish and stool samples were identified with the following system. These strains were primarily identified with API 20E (Biomérieux). Then growth tests at 4 and 42°C (16, 18) and assimilation tests of four carbon substrates (14) were carried out for the final identification to the species level. The incubation times for the growth tests at 4 and 42°C were 7 and 14 days, respectively. The four carbon substrates were ethanolamine, histamine, D-melezitose, and DL-β-hydroxybutyric acid (Sigma Chemical Co., St. Louis, Mo.). In addition to the above-mentioned strains isolated at the Osaka Prefectural Institute of Public Health, 17 provided strains were investigated (2 strains of *R. planticola*, 5 strains of *R. ornithinolytica*, 1 strain of *Raoultella terrigena*, 8 strains of *K. pneumoniae,* and 1 strain of *K. oxytoca*). We also examined the following 13 reference strains: *R. planticola* ATCC 43176 (American Type Culture Collection), IFO 3317 (Institute for Fermentation, Osaka, Japan), and IFO 14939; *R. ornithinolytica* ATCC 31898, JCM 7522 (Japan Collection of Microorganisms, Saitama, Japan), and JCM 7523; *R. terrigena* ATCC 33628 and IFO 14941; *K. pneumoniae* subsp. *pneumoniae* IFO 3512 and IFO 14940; *K. oxytoca* JCM 1665; *K. pneumoniae* subsp. *ozaenae* JCM 1663; and *K. pneumoniae* subsp. *rhinoscleromatis* JCM 1664. *Morganella morganii* JCM 1672 and *Enterobacter aerogenes* JCM 1235 were also employed as other HPB known to possess similar *hdc* genes (10, 23).

* Corresponding author. Mailing address: Osaka Prefectural Institute of Public Health, Nakamichi 1-3-69, Higashinari-ku, Osaka 537-0025, Japan. Phone: 81-6-6972-1321. Fax: 81-6-6972-1329. E-mail: kanki@iph.pref.osaka.jp.

TABLE 1. Number of positive reactions for the growth and assimilation tests of 145 strains

Organism	No. of strains tested	No. of positive reactions					
		Growth test at:		Assimilation test with:			
		42°C	4°C	Ethanolamine	Histamine	D-Melezitose	DL-β-Hydroxybutyric acid
R. planticola	48	48	46	0	46	0	48
R. ornithinolytica	13	13	13	0	13	0	12
R. terrigena	3	0	2	0	3	3	3
K. pneumoniae subsp. *pneumoniae*	61	61	0	53	0	0	61
K. oxytoca	18	18	0	18	0	16	0
K. pneumoniae subsp. *ozaenae*	1	1	0	0	0	0	0
K. pneumoniae subsp. *rhinoscleromatis*	1	1	0	0	0	0	1

Histamine analysis of the *Raoultella* strains. After cultivation overnight in Trypticase soy broth, aliquots (10 μl) of the bacterial cultures were transferred into 2 ml of Trypticase soy broth fortified with 1.0% histidine, pH 5.8 (TSBH) (22), and incubated at 30°C for 18 h. One-hundred-microliter aliquots were removed from each medium for measurement and diluted with distilled water (1:10 and 1:20 dilutions), and the histamine levels were measured with Histamarine (Immunotech, Marseille, France), an enzyme-linked immunosorbent assay kit, according to the manufacturer's protocol.

PCR amplification of the *hdc* genes. The primers KPF2 (5′-AAA GCT GGG GGT ATG TGA CC-3′) and KPR4 (5′-GTG ATG GAG TTT TTG TTG C-3′) were designed on the basis of the *hdc* genes of *R. planticola* (GenBank and EMBL accession no. M62746). DNA amplification by PCR was performed in a reaction volume of 50 μl containing 0.75 U of Z-*Taq* DNA polymerase (Takara Biomedicals, Shiga, Japan), 25 pmol of each primer, and 5 μl of sample DNA purified by the benzyl alcohol-guanidine hydrochloride organic extraction method (7). Initial denaturation was carried out for 2 min at 94°C, and then 30 cycles of amplification were performed on a DNA thermal cycler (model 2400; PE Biochemicals Inc., Norwalk, Conn.). Each cycle consisted of three steps: denaturation for 5 s at 98°C, annealing for 5 s at 62°C, and extension for 5 s at 72°C. An additional step of extension for 5 min at 72°C was performed at the end of the amplification to complete the extension of the primers. Amplification products were detected by electrophoresis on a 1.5% agarose gel.

Preparation of the probe for the *hdc* genes. A probe was prepared by PCR with genomic DNA of *R. planticola* ATCC 43176 as a template with the primers KPF5 (5′-TGC TAT CTG GGT CGG GAG AT-3′) and KPR6 (5′-ATG CCC AGT TCG CTA ATT GA-3′). Labeling of the probe was achieved with a PCR digoxigenin probe synthesis kit (Roche Diagnostics Co., Mannheim, Germany).

Southern blot hybridization. Genomic DNA was prepared with a DNeasy tissue kit (QIAGEN Inc., Chatsworth, Calif.), and 0.5 μg of the DNA was completely digested with restriction enzymes, electrophoresed on a 0.7% agarose gel, and vacuum transferred to a GeneScreen Plus membrane (NEN Life Science Products, Inc., Boston, Mass.). The membrane was prehybridized in ExpressHyb hybridization solution (Clontech Laboratories, Inc., Palo Alto, Calif.) at 50°C for 30 min, followed by hybridization at 50°C overnight with the same solution containing a probe labeled with 10-ng/ml digoxigenin. The hybridized probe on the membrane was detected by alkaline phosphatase-conjugated anti-digoxigenin antibody (Fab; Roche Diagnostics Co.). The enzyme-catalyzed color reaction was carried out with a nitroblue tetrazolium salt (NBT)–5-bromo-4-chloro-3-indolylphosphate (BCIP) system (Roche Diagnostics Co.).

Direct sequencing of the *hdc* PCR products. The amplified DNA was directly sequenced with a BigDye terminator cycle sequencing FS Ready Reaction kit (PE Biochemicals Inc., Foster City, Calif.). The sequence of the labeled DNA sample was read by an ABI PRISM 310 genetic analyzer (PE Biochemicals Inc.) and analyzed with Factura software (PE Biochemicals Inc.).

Nucleotide sequence accession numbers. The partial *hdc* sequence data for seven *Raoultella* strains reported in this study have been submitted to the DDBJ database and assigned accession no. AB075216 to AB075222 (inclusive).

RESULTS

Identification of nonmotile strains from fish and stool specimens. Twenty-seven strains from fish were identified as *R. planticola* (22 strains) and *R. ornithinolytica* (5 strains). Eighty-eight strains from stool samples were identified as *R. planticola* (21 strains), *K. pneumoniae* (51 strains), and *K. oxytoca* (16 strains). The identification results for a total of 145 strains are indicated in Table 1.

All the strains of *R. planticola*, most of which were able to grow at 4°C (46 of 48 strains) and utilize histamine (46 of 48 strains) and all of which utilized DL-β-hydroxybutyric acid but not ethanolamine and D-melezitose (48 of 48 strains), were misidentified as *K. pneumoniae* or *K. oxytoca* by the API 20E system. A total of 48 strains of *R. planticola* and 13 strains of *R. ornithinolytica* are listed in Table 2. Thirty-six (17 strains from fish, 16 strains from stool specimens, and 3 provided and reference strains) of the 48 *R. planticola* strains showed a positive reaction to an indole production test.

Histamine production by *Raoultella* strains. All the strains from fish (22 strains of *R. planticola* and 5 strains of *R. ornithinolytica*) produced between 2,810 and 5,250 mg of histamine per liter in TSBH (Table 2).

In 88 strains of stool origin, 15 of 21 *R. planticola* strains produced between 2,610 and 5,200 mg of histamine per liter. The rest of the *R. planticola* strains (6 strains) and all the strains of *K. pneumoniae* (51 strains) and *K. oxytoca* (16 strains) produced no histamine.

With the 17 provided and 13 reference strains, 3 of 5 strains of *R. planticola* and all 8 strains of *R. ornithinolytica* also produced between 3,370 and 5,130 mg of histamine per liter. The rest of the *R. planticola* strains (2 strains) and all the strains of *R. terrigena* (3 strains), *K. pneumoniae* (10 strains), *K. oxytoca* (2 strains), *K. pneumoniae* subsp. *ozaenae* (1 strain), and *K. pneumoniae* subsp. *rhinoscleromatis* (1 strain) produced no histamine.

PCR detection of *hdc* genes. Positive PCR results were obtained from all the histamine-producing strains (40 strains of *R. planticola* and 13 strains of *R. ornithinolytica*) (Fig. 1). Among the strains that produced no histamine (8 strains of *R. planticola*, 3 strains of *R. terrigena*, 61 strains of *K. pneumoniae*, 18 strains of *K. oxytoca*, 1 strain of *K. pneumoniae* subsp. *ozaenae*, and 1 strain of *K. pneumoniae* subsp. *rhinoscleromatis*), only 2 strains of indole-positive *R. planticola* (strains S8 and SJ10) showed positive PCR results. Regardless of histamine production, all 36 strains of indole-positive *R. planticola* showed positive results by PCR, as indicated in Fig. 1.

Southern blot hybridization. Genomic DNAs of *R. planticola* ATCC 43176, *R. ornithinolytica* ATCC 31898, *M. morganii* JCM1672, and *E. aerogenes* JCM1235 were digested with three restriction enzymes (*Eco*RI, *Fsp*I, and *Pst*I) and used as the

TABLE 2. Characteristics of the *R. planticola* and *R. ornithinolytica* strains studied

Strain	Source	Indole production	Histamine production (mg/liter)	PCR response
R. planticola				
19-3	Fish	+	4,650	+
27-1	Fish	+	4,340	+
46-1	Fish	+	4,220	+
50-4	Fish	+	4,210	+
51-1	Fish	+	4,680	+
54-1	Fish	+	4,350	+
55-1	Fish	+	4,390	+
56-1	Fish	+	4,690	+
57-1	Fish	+	4,530	+
103-1	Fish	+	3,440	+
107-1	Fish	+	3,490	+
111-1	Fish	+	3,990	+
117-1	Fish	+	4,720	+
129-1	Fish	+	4,690	+
130-1	Fish	+	3,850	+
138-5	Fish	+	3,360	+
F1-1	Fish	+	4,030	+
F14	Stool	+	3,280	+
F27	Stool	+	4,700	+
F39	Stool	+	4,420	+
I5	Stool	+	2,980	+
I9	Stool	+	2,920	+
I20	Stool	+	2,860	+
I22	Stool	+	3,410	+
I27	Stool	+	2,980	+
I30	Stool	+	2,610	+
S18	Stool	+	2,920	+
S22	Stool	+	3,260	+
SJ1	Stool	+	3,140	+
SJ11	Stool	+	3,110	+
SJ16	Stool	+	2,780	+
S8	Stool	+	<1	+
SJ10	Stool	+	<1	+
492	Provided	+	4,650	+
ATCC 43176		+	4,550	+
IFO 3317		+	3,550	+
28-1	Fish	−	5,250	+
42-1	Fish	−	4,230	+
Y1-1	Fish	−	2,810	+
117-3	Fish	−	5,090	+
140-1	Fish	−	4,350	+
SJ9	Stool	−	5,200	+
F36	Stool	−	<1	−
I12	Stool	−	<1	−
S13	Stool	−	<1	−
SJ17	Stool	−	<1	−
493	Provided	−	<1	−
IFO 14939		−	<1	−
R. ornithinolytica				
19-2	Fish	+	4,210	+
46-4	Fish	+	4,940	+
57-7	Fish	+	4,640	+
010-1	Fish	+	4,280	+
107-5	Fish	+	3,480	+
624	Provided	+	3,940	+
625	Provided	+	5,130	+
626	Provided	+	3,370	+
627	Provided	+	3,580	+
628	Provided	+	3,770	+
ATCC 31898		+	4,660	+
JCM 7522		+	4,190	+
JCM 7523		+	3,510	+

reference strains in Southern hybridization experiments with the detection probe for the *hdc* genes. Hybridization signals were observed for four strains (Fig. 2). In both *R. planticola* and *R. ornithinolytica*, the probe hybridized to DNA fragments of 9.9 kbp when the DNAs were digested by *Eco*RI, 5.5 and 2.4 kbp when they were digested by *Fsp*I, and 1.8 kbp when they were digested by *Pst*I. Since there is an *Fsp*I site within the probe-hybridizing area of *R. planticola* ATCC 43176, two fragments (5.5 and 2.4 kbp) were observed with this enzyme as expected. The patterns obtained from *R. planticola* ATCC 43176 and *R. ornithinolytica* ATCC 31898 were congruent.

The genomic DNAs of 92 non-histamine-producing strains were digested with *Pst*I for detection of the *hdc* genes. The *hdc* probe hybridized to 1.8-kbp DNA fragments of only two strains of *R. planticola*, S8 and SJ10. The lengths of the hybridized fragments in these two strains were equivalent to those of the fragments in the reference strains of *R. planticola* and *R. ornithinolytica* digested with the same restriction enzyme, *Pst*I. The results of the PCR tests corresponded well with those of the hybridization.

Direct sequencing of PCR products. PCR products from six strains of *R. planticola* (19-3, 27-1, 28-1, 42-1, Y1-1, and S8) and one strain of *R. ornithinolytica* (19-2) were sequenced and compared with the sequence of *R. planticola* ATCC 43176 (GenBank and EMBL accession no. M62746). The partial nucleotide sequence (685 bp) of the PCR products from the seven strains showed 97.2 to 99.4% identity to *R. planticola* ATCC 43176. Furthermore, *R. planticola* strain S8 and *R. ornithinolytica* strain 19-2 showed 100% identity.

DISCUSSION

The histamine-producing strains were identified as *R. planticola* (40 strains) and *R. ornithinolytica* (13 strains), whereas a total of 61 strains of *K. pneumoniae* and 18 strains of *K. oxytoca* produced no histamine in TSBH and gave negative results for PCR and DNA hybridization of the *hdc* genes. A group of histamine-producing strains were classified as *K. pneumoniae* when Taylor et al. and Niven et al. reported HPB in fish in 1979 and 1981, respectively (17, 20). Afterward, this group's identification was changed from *K. pneumoniae* and *K. oxytoca* to *K. planticola* and *K. ornithinolytica* when *K. planticola* and *K. ornithinolytica* were distinguished from *K. pneumoniae* and *K. oxytoca* as new species. These two *Klebsiella* species have since been classified in the genus *Raoultella*.

K. pneumoniae and *K. oxytoca* have been considered to be the most important HPB isolated from fish even after *K. planticola* was described as a new species (12, 13). So far, *R. planticola* has not been reported as an HPB, except in the case of one strain, ATCC 43176 (8). Histamine-producing strains of *R. planticola* appear to have been misidentified as either *K. pneumoniae* or *K. oxytoca* by conventional methods used in the identification of HPB (11, 13). *R. planticola* cannot be distinguished from *K. pneumoniae* and *K. oxytoca* with the commercialized systems, because *K. planticola* (*R. planticola*) is not included in the databases of these systems (14). In fact, 48 collected strains of *R. planticola* were misidentified as *K. pneumoniae* or *K. oxytoca* by the API 20E system. *R. ornithinolytica* has also not been reported as an HPB, although commercialized systems are able to identify it. However, *R. ornithinolytica*

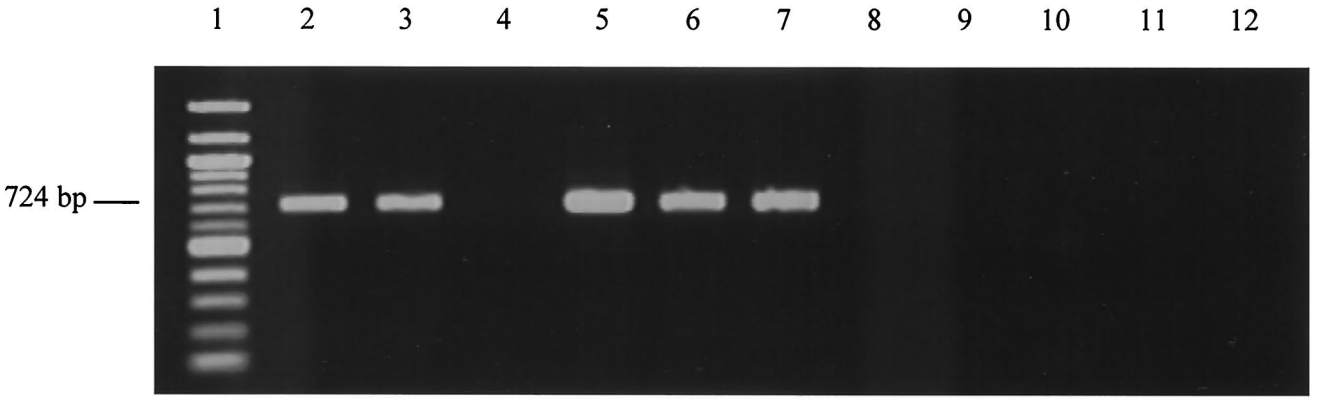

FIG. 1. Amplification of DNA from *Raoultella* strains with the primers KPF2 and KPR4. Lane 1, molecular size markers (100-bp DNA ladder by New England BioLabs); lane 2, *R. planticola* ATCC 43176; lane 3, *R. planticola* IFO 3317; lane 4, *R. planticola* IFO 14939 (non-histamine-producing strain); lane 5, *R. ornithinolytica* ATCC 31898; lane 6, *R. ornithinolytica* JCM 7522; lane 7, *R. ornithinolytica* JCM 7523; lane 8, *K. pneumoniae* IFO 14940; lane 9, *K. pneumoniae* IFO 3512; lane 10, *K. oxytoca* JCM 1665; lane 11, *R. terrigena* ATCC 33628; lane 12, *R. terrigena* IFO 14941.

was isolated as an HPB from fish and was found in the present study to be equivalent to *R. planticola* in its histamine-producing ability.

We demonstrated the importance and efficiency of Monnet and Freney's method for the identification of histamine-producing *Raoultella* strains (14). For the histamine assimilation test, *R. planticola* and *R. ornithinolytica* gave positive results but *K. pneumoniae* and *K. oxytoca* gave negative results. It is rea-

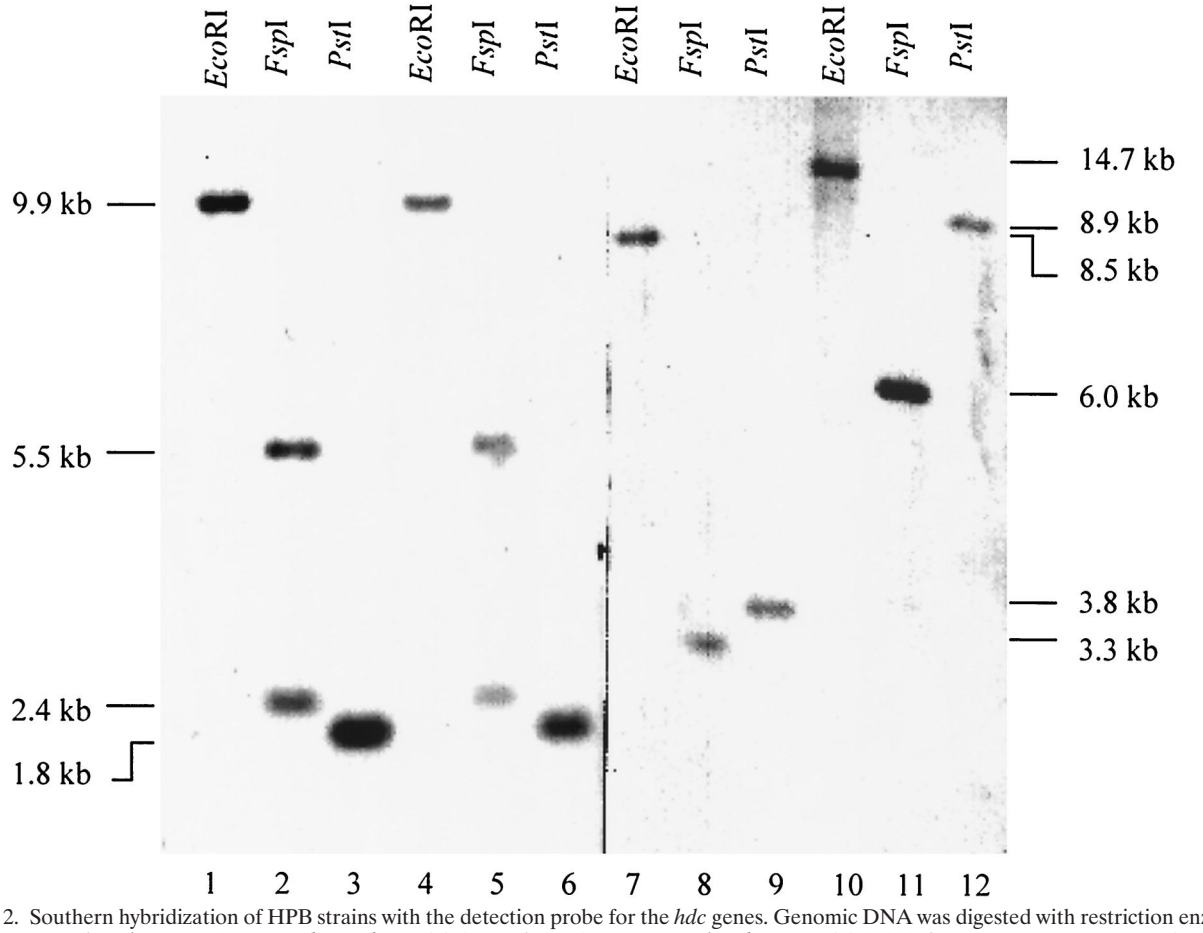

FIG. 2. Southern hybridization of HPB strains with the detection probe for the *hdc* genes. Genomic DNA was digested with restriction enzymes (*Eco*RI, *Fsp*I, and *Pst*I). Lanes 1 to 3, *R. planticola* ATCC 43176; lanes 4 to 6, *R. ornithinolytica* ATCC 31898; lanes 7 to 9, *M. morganii* JCM 1672; lanes 10 to 12, *E. aerogenes* JCM 1235.

sonable to postulate that histamine-utilizing species (*R. planticola* and *R. ornithinolytica*) are able to produce histamine and that non-histamine-utilizing species (*K. pneumoniae* and *K. oxytoca*) are unable to produce histamine. Another histamine-utilizing *Raoultella* species, *R. terrigena*, produced no histamine, although only three strains were investigated. *R. terrigena* was isolated mainly from nonclinical origins (soil and water) (9). It may be that *R. terrigena* contaminates fish; however, *R. terrigena* strains were not isolated as HPB from fish in the present study.

R. planticola and *R. ornithinolytica* are able to grow slowly at 4°C. Moreover, these strains are often isolated from raw fish and fish products. The low-temperature growth response and environmental distribution of histamine-producing *Raoultella* strains are notable with regard to food hygiene. There was no difference in the histamine-producing capabilities among the histamine-producing strains regardless of their sources. All the histamine-producing *Raoultella* strains produced a large amount of histamine. There is little doubt that *R. planticola* and *R. ornithinolytica* are the most important HPB that cause HFP.

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